Geographic variation in Douglas-fir from the Coastal ranges of California

II. Predictive Value of a Regression Model for Seedling Growrh Variation

By A. R. Griffin*)

Summary

Douglas-fir seedlings from the coastal ranges of California were grown in a nursery at Corvallis, Oregon, and epicotyl length determined at the end of the first growing season.

A regression model based on source elevation, latitude, and distance from the ocean successfully described the between-stand pattern of variation ($r^2 = 0.88$).

Height growth data from two independent collections of seedlots from the same area were used to test the validity of the model. At age 13, the height of 14 seedlots grown in field trials in New Zealand was correlated with values predicted by the model ($r = 0.89$), while for a sample of equal size grown for 2.5 years in a Tasmanian nursery a similar correlation was observed ($r = 0.88$).

Applications to producing seed seea zone maps and to reducing provenance field testing requirements are discussed, together with the limitations and possibilities for the more general application of early testing techniques.

Key *words:* Douglas-fir; provenance testing; juvenile-mature correlation; height growth.

Zusammenfassung

Am Ende der ersten Vegetationsperiode wurde bei Douglasien-Sämlingen aus kalifornischen Küstenherkünften, die in einer Baumschule bei Corvallis angezogen worden waren, die Epikotyllänge gemessen. Mit Hilfe eines auf Höhenlage, geogr. Breite und Entfernung zur Küste der Herkunftsorte basierenden Regressionsmodells gelang es, die Variationsmuster zwischen Beständen ($r^2 = 0{,}88$) zu beschreiben. Um die Brauchbarkeit des Modells nachzuprüfen, wurden Höhenwachstums-Daten von zwei unabhängigen Stichproben gleicher Herkunft verwendet. Im Alter 13 war die Höhe von 14 in Neuseeland angebauten Herkünften mit den mittels des Modells vorausgerechneten Werten korreliert ($r = 0{,}89$). Eine ähnliche Korrelation ($r = 0{,}88$) wurde bei einer Stichprobe gleicher Größe nach drei Vegetationsperioden in Tasmanien festgestellt. Die Anwendung des Verfahrens bei der kartographischen Darstellung von Samenzonen und bei der Vereinfachung von Feldprüfungsvoraussetzungen sowie die Grenzen und Möglichkeiten einer allgemeinen Anwendung von Frühtestmethoden werden besprochen.

Introduction

The first paper in this series (Griffin and Ching 1977) discussed variation in a number of seed and seedling characteristics of Douglas-fir from the coastal ranges of northern California. The analysis of variance of data obtained from the growth of seedlings raised in a nursery at Corvallis, Oregon, was used to verify the existence of genetic differences between populations, and to identify the scale on which selection pressures were operating. This paper presents a multiple regression model describing the pattern of geographic variation in epicotyl length after one growing season in terms of source location indices.

Height growth is an easily measured index of productivity and one for which, at least at a given site, provenance ranking remains consistent over the early part of a rotation (Rowe and Ching 1973). If provenance X planting site interactions are not of major importance, and the regression model baced on nursery performance truly reflects genetic differentiation within the species, then the regression model should be useful in predicting performance of seed collected from anywhere within the area on which the model is based.

Seedlings raised in Australia and New Zealand, from two independent seed collections, provide data for testing this proposition.

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Methods

Sampling

Sampling was designed to cover the geographic distributi m of the species within the definod study area (Griffin and Ching 1977). Since the steepest environmental gradients run inland from the Pacific coast, collections were made at up to three locations along an east-west transect at each of four latitudinal intervals (*Figure* 1, Table 1). The varying number of locations sampled in each transect reflects the greater environmental range of the species in the northern part of the study area. At each location the species' elevatimal range was sampled, ideally with eone collections from two trees per 250 ft. interval.

Nursery Procedures.

Seedlings were grown in 2-inch styroblock containers under three different watering regirnes, and various growth and phenology traits observed over the first growing season. Mean epicotyl length per family over all watering regimes and replications (36 seedlings assuming complete survival) was the variable of interest for this regression

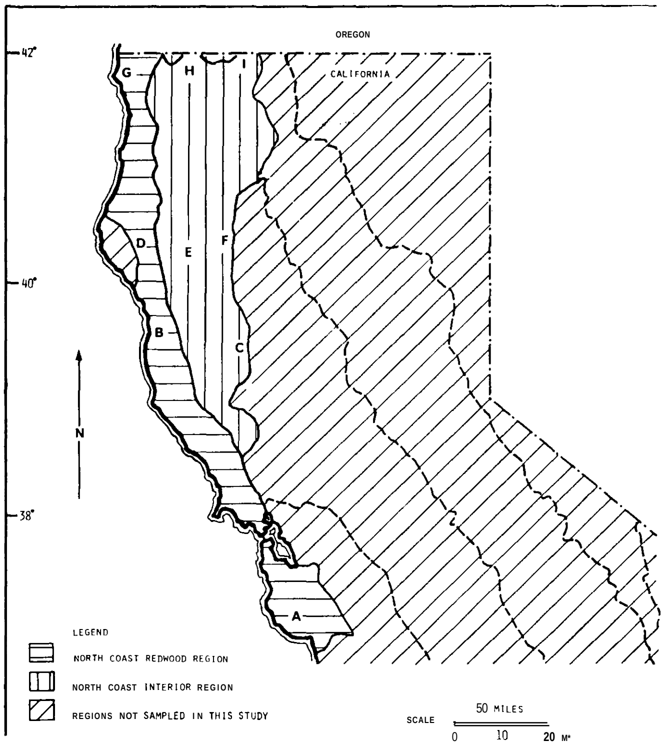

Figure 1. — Physiographic and climatic regions of northern California (after California Tree Seed Zone Map, Buck et al. (1970)), showing sampling locations (A. . . . . I).

Table 1. — Average location indices, and epicotyl length for the nine major sampling locations

Location		Latitude (N) °	'	Longitude (W) °	'	Distance from Ocean (Miles)	Elevation (ft.)	No. Stands	Total No. Parent Trees	Epicotyl Length (cm)
Gasquet	(G)	41	47	124	00	7	1847	10	19	2.43
Happy Camp	(H)	41	52	123	28	36	2437	15	34	1.17
Mt. Ashland	(I)	41	56	122	47	74	3238	11	26	0.98
Humboldt Redwood State Park	(D)	40	14	124	00	16	1490	12	22	1.94
Forest Glen	(E)	40	23	123	23	42	3532	8	14	1.17
Harrison Gulch	(F)	40	20	123	00	58	3567	4	9	1.00
Jackson State Forest	(B)	39	32	123	36	11	1250	10	19	2.49
Bear Creek (Mendocino N.F.)	(C)	39	17	122	50	50	3290	6	11	1.25
Santa Cruz	(A)	37	08	122	11	5	1292	9	27	2.33

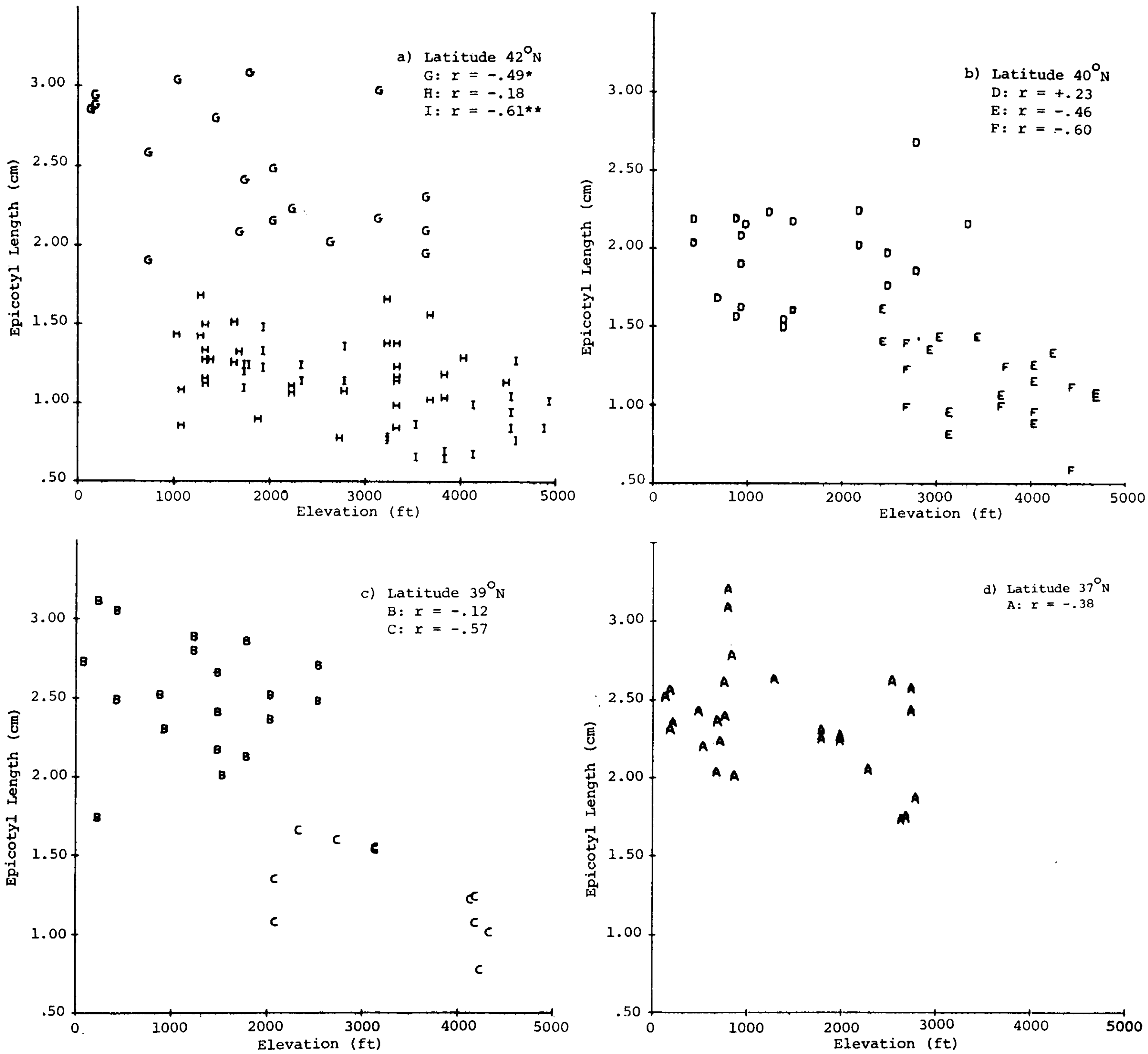

Figure 2 (a—d). — Variation of epicotyl length with elevation by latitudinal transects and sample locations. Each point represents a family mean.

analysis. These are listed in GRIFFIN 1974 (unpubl.) and mean values for all seedlings from each location given in *Table 1.*

Choice of Location Indices.

Previous regression analyses of variation in Douglas-fir (e.g. SWEET 1965, BIROT 1972, HATTEMER and KÖNIG 1975) have used latitude, longitude, and elevation as independent location indices. *Latitude* determines day length and, to a lesser extent in California, temperature. Longitude broadly reflects the degree of continentality of climate in the western U.S.A., however, since sampling in this study was restricted to the coastal mountains, *distance from the ocean* was considered to be a more useful index of this aspect of the environment. It would, of course, have little utility if one wished to extrapolate across the Sacramento Valley to the Sierra Nevada populations, or analyse comparable sample transects further north where the Willamette Valley and Puget Sound cause more complex patterns of climatic variation.

Regional heterogeneity of the height growth/elevation regression (HATTEMER and KÖNIG 1975) show the inadequacy of elevation *per se* as an environmental index, and such heterogeneity also exists within the study area — a minor part of a "region" in HATTEMER and KÖNIG's terms. For example epicotyl growth of seedlings from 1500 ft at location (G) was about twice as great as that of seedlings from an equivalent elevation 35 miles further inland at the same latitude (H) *(Figure 2).* Nevertheless within a given location seedlings did show a tendency for reduced growth with increasing source *elevation,* so the latter was included as an additional independent variable, together with a range of interaction terms. Since families within the same stand had identical location indices the regression model represents the between-stand variation accounted for by the independent variables, and it is possible to separate the residual stand-to-stand variation from that due to families within stands.

Results

Regression Model

The REGRESS sub-system of the O.S.U. Computer Centre SIPS system was used for stepwise multiple regression analysis of epicotyl length on the location indices, their second order powers, and cross-products.

The best model *(Table 2)* according to this procedure confirms the large geographic variation component for this trait ($r^2 = 0.88$), though the residual stand-to-stand variation is still statistically significant. Because of the co-variances which exist between the independent variables it is not strictly meaningful to discuss the independent contribution of each to the complete model. Nevertheless, if the latter is to be a useful aid to seed movement decisions, then interpretation in biological terms should be possible.

The most important primary location index, as judged by preliminary simple correlation analysis, is distance from the ocean ($r = -0.83$). A plot of epicotyl length against distance *(Figure 3)* reveals a non-linear clinal variation pattern with the greatest rate of change about 25—35 miles inland, corresponding to the inner limit of the moderating coastal influence. This is reflected in the model by inclusion of the second order distance terms. Growth also decreases

Table 2. — Epicotyl length regression on location indices

Model:

$$Y = -2.5224 + 0.1336X_1 - 0.000098X_2 + 0.614X_3 - 0.01614X_1X_3 - 0.00869X_3X_3 + 0.00022X_1X_3X_3$$

where Y = Epicotyl length (cm) X_1 = Latitude (°N)

X_2 = Elevation (ft.) X_3 = Distance from ocean (miles)

Analysis of Variance

Source of Variation	d.f.	S.S.	M.S.	F.
Regression	6	66.441	11.07	115.83**
Residual	78	9.277	0.1189	1.55*
Families	96	7.361	0.0767	
	180	83.079		

$r = 0.937$ $r^2 = 0.877$

t-Tests of Coefficients:

Variable	S.E. of Coefficient	t
X_1	0.0274	4.87**
X_2	0.000024	-4.01**
X_3	0.1097	5.60**
X_1X_3	0.0027	-6.06**
X_3X_3	0.0019	-4.53**
$X_1X_3X_3$	0.000046	4.77**

Table 3. — Location mean residuals as a percentage of observed mean epicotyl length (positive values indicate observed > predicted)

G	+2.8	H	+0.6	I	-0.3
D	-12.1	E	-4.7	F	+5.7
B	+10.2	C	+2.8		
A	-0.8				

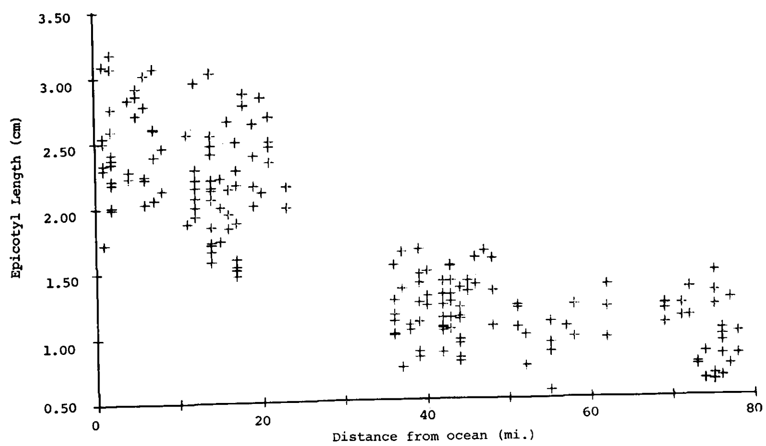

Figure 3. — Variation of epicotyl length with distance from the ocean. Each point represents a family mean.

Table 4. — Locations indices and observed height values for independent samples and values predicted by regression model

Seedlot No.	Sample Location	Latitude ° '	Mean Elevation (ft.)	Distance from Ocean (Miles)	Observed Height (cm)			Predicted Epicotyl Length (cm)
					Tasmania (2.5 yrs.)	New Zealand (2 yrs.)	New Zealand (13 Yrs.)	
1104*	Brookings	42 07	1000	5	84.6	-	-	2.69
1126	Ashland	42 05	4900	84	48.3	-	-	1.15
1127	Happy Camp	41 57	3200	36	52.6	-	-	1.20
1128	Gasquet	41 51	400	12	86.4	-	-	2.37
12 (642)+	Berteleda	41 48	300	6	-	54.9	1060	2.69
1134	Sawyers Bar	41 17	3800	50	60.2	-	-	0.99
14 (644)	Lamoine	40 59	1600	88	-	30.0	730	1.14
15 (645)	Willow Creek	40 57	600	26	-	40.4	920	1.89
16 (646)	Six Rivers	40 55	1600	13	-	48.8	890	2.24
1138	Arcata	40 55	1600	12	84.6	-	-	2.28
17 (647)	Mad River	40 55	700	11	-	51.6	1060	2.40
1139	Weaverville	40 54	3750	70	68.6	-	-	0.85
1140	Arcata	40 54	2900	19	75.4	-	-	1.89
1143	Wildwood	40 23	3900	56	56.6	-	-	0.99
18 (648)	Miranda	40 14	1700	15	-	56.6	910	2.19
1144	Covelo	39 55	3000	30	66.0	-	-	1.69
21 (651)	Mendecino N.F.	39 51	4500	45	-	-	780	1.20
20 (650)	Mendecino N.F.	39 50	2500	40	-	47.2	880	1.51
1145	Covelo	39 48	5100	47	56.6	-	-	1.11
19 (649)	Dehaven	39 36	500	2	-	63.0	980	2.67
1148	Willitts	39 23	1800	22	73.7	-	-	2.08
24 (654)	Jackson S.F.	39 21	500	4	-	62.2	1040	2.60
1149	Lower Lake	38 50	3100	37	67.8	-	-	1.69
27 (657)	Middletown	38 46	1500	33	-	43.9	860	1.95
28 (658)	Stewarts Point	38 39	500	2	-	62.2	1020	2.57
29 (659)	Stinson Beach	37 53	800	2	-	-	1040	2.46
S10896·	Swanton	37 05	500	2	82.0	-	-	2.42
30 (660)	Santa Cruz	37 05	1000	2	-	76.7	1070	2.36

* 4 — digit numbers — IUFRO Seedlot No. (Birot 1972)
\+ Numbers of this form — Sweet (1965), and Wilcox (1974) (unpubl.)
. Rout (1973) unpubl.

with elevation, while the latitudinal effect cannot be stated concisely because of the significant interaction with distance terms. These are best considered as a result of the species distribution, and hence sampling scheme *(Figure 1)*, rather than indicating differential adaptive responses, since the interior limit of Douglas-fir is progressively nearer the coast as latitude decreases. The model does emphasize that, as with the elevational effects discussed above, it is not possible to make unqualified statements about the species' latitudinal variation pattern *per se*.

The fit of the model over the whole study area was tested by predicting epicotyl length for each family, and determining the mean deviation of predicted and observed values for families at each of the nine locations *(Table 3)*. The major defect is that values for location (D) (Humboldt Redwood S.P.) are over-estimated, with the reverse true for (B) (Jackson State Forest). All other predictions fell within 6% of observed values. (D) is only 16 miles from the ocean, yet because of the barrier formed by Cape Mendicino the influence of coastal air masses is not direct, but from the north-west through the Eel River Valley. At (B) the topography rises gradually from the coast and west-facing slopes are exposed to direct ocean influence for some 20 miles inland, so most collection sites were probably more mesic than would be inferred from the distance index.

Predictive Value of the Model.

Data from trials in New Zealand and Australia, based on two independent seed collections within the study area (Sweet 1965, Wilcox 1974 unpubl., Rout 1973 unpubl.), provided a test of the predictive value of the model.

Reported latitude, longitude, and elevation were used to identify the location of each sample on a 1 : 500,000 map of California, and minimum distance to the ocean was determined. Predicted epicotyl length values for each location were then derived from the regression equation. The correlation coefficient for predicted epicotyl length and observed height growth in the nursery or field trials was used to assess the utility of the model.

The three sets of data used for this test were:

i) 2-year height of 12 of the provenances collected in 1956 and grown in a nursery at Rotorua, New Zealand (Sweet 1965).
ii) Average 13-year height of 14 provenances from the same collection when planted on 6 sites throughout New Zealand (Wilcox 1974, unpubl.).
iii) 2.5-year height of 14 of the provenances collected by I.U.F.R.O. (1966—69) and grown in a nursery in Tasmania, Australia (Rout 1973, unpubl.).

In each of the the three cases the linear correlation of predicted epicotyl length and observed nursery or field height growth was statistically significant *(Figure 4)*. For the New Zealand studies the increased r value for correlation with 13-year height compared with 2-year nursery height of the same seedlots was due to the unexpectedly fast nursery growth of seedlot 30 (Santa Cruz). In the field trials this seedlot was still the tallest, but not significantly different from a number of other coastal seedlots. This is reflected in a correlation coefficient of only $r = 0.81$ for the 2-year and 13-year New Zealand results.

The model predictions correlate with nursery growth of the IUFRO seedlots raised in Tasmania with comparable precision. The seedlots which showed the greatest departure from expectation were 1126 (Ashland) and 1139 (Weaverville). These were both on the periphery of the area sampled, and illustrate the breakdown of predictive value once extrapolation is attempted.

Discussion

Application of Results

The analyses show that first year nursery data can be used to predict subsequent relative growth potential of Douglas-fir provenances from the northern Californian coast ranges. As the New Zealand and Australian data refer to independent seed collections from different stands of trees, there is strong evidence that the various environmental gradients approximated by the location indices are continuous throughout the study area, and have resulted

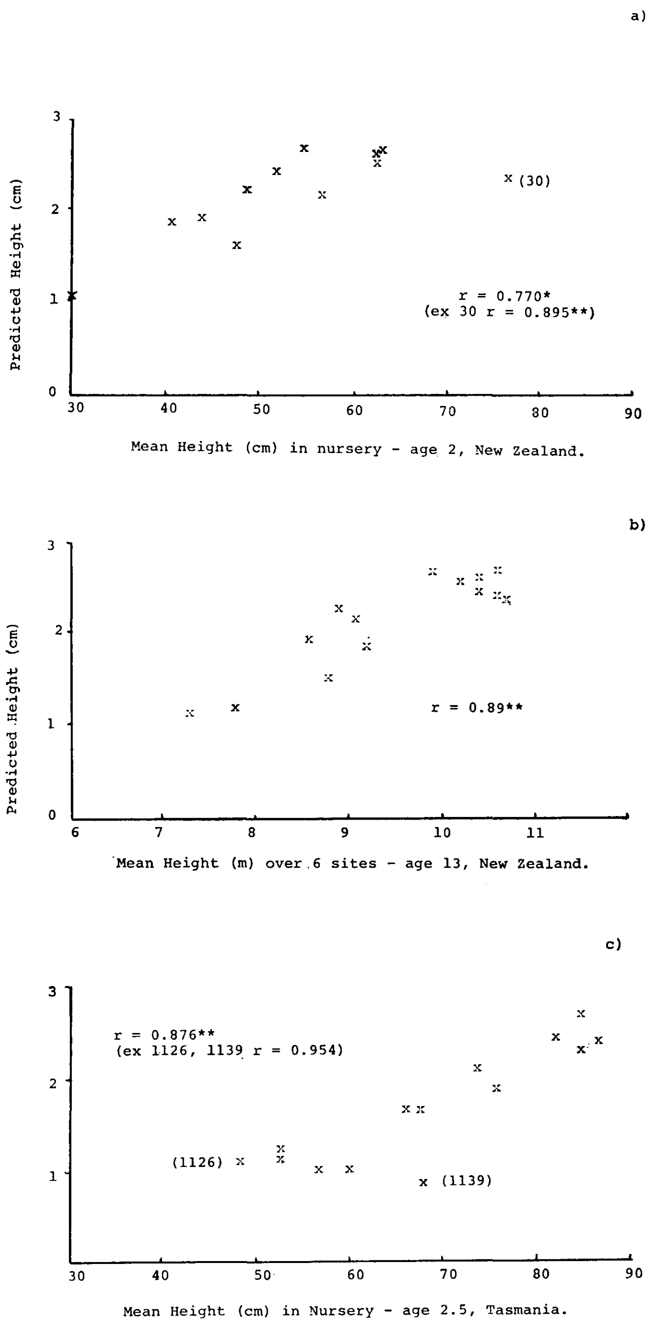

Figure 4 (a—c). — Scatter diagramf of predicted epicotyl length and observed height growth in New Zealand and Tasmania.

in corresponding clinal differentiation of the Douglas-fir population.

The ability to predict relative height growth at 13-years confirms that provenance rankings do not change markedly over the early years of the rotation (Sziklai 1966, Rowe and Ching 1973). Because the extent to which height growth is itself a satisfactory index of crop volume production will depend upon the survival as well as individual tree growth (Silen 1966), predictions are likely to be most useful for plantations on mesic sites. Neither drought nor severe winter cold are characteristic of the New Zealand field test sites.

The regression model may be useful in two ways. Firstly it could be used to define the seed zone boundaries within the study area. Given topographic information the equation could be solved to produce a map of "iso-growth-potential" contours. The closeness of iso-lines would indicate areas where zone boundaries should be defined. Secondly it could be used for the preliminary assessment of seedlots, and hence to reduce the size of field provenance trials. For example the most vigorous 50% of the 14 seedlots in the 13-year New Zealand sample could have been correctly predicted, though not their ranking relative to each other. 6 of the 7 most vigorous seedlots in the Tasmanian trial could have been similarly predicted.

The ultimate step of eliminating field testing could be taken if resources are limited, or if early vigour is the sole trait of interest. In most cases field planting will still be required to assess other traits such as wood properties and resistance to pathogens — though early tests could of course also be developed for these.

General Acceptability of Procedures.

As the model has greater predictive value than many others reported in the literature it is worthwhile considering the extent to which the sampling and nursery procedures and the choice of independent variables may be applicable to other species and environments.

The seedlings on which the model was based were raised in containers under sub-optimal conditions (Griffin and Ching 1977) — as evidenced by the first year average epicotyl growth of only 1.7 cm — and this allowed expression of genetic variation in growth patterns which may not be observed until the second and subsequent growing seasons under a more normal nursery regime. In this regard it is noteworthy that predicted values correlated better with second year nursery growth in the New Zealand study (Sweet 1965) (r = 0.77*) than with first year growth (r = 0.54 n.s.) (Griffin 1974 unpubl.). Because the seedlings were small with hypocotyl length forming a significant part of total seedling height, and because seed size effects resulted in a negative correlation between hypocotyl and epicotyl length (Griffin and Ching 1977), it was important that only the epicotyl growth, rather than total height, was used in constructing the regression model.

The ability to develop useable regression models will vary with the genecology and distribution of the species, and associated environmental gradients, and the choice of appropriate independent variables will also vary. For example the index "distance from the ocean" was chosen for this particular study because it reflected a climatic gradient (Griffin 1974 unpubl.). It would be far less useful for more northerly parts of the coastal Douglas-fir range where topography induces more complex environmental gradients. Within the northern coast ranges the model predicts a minimum growth depending on latitude and elevation, at 70—90 miles from the coast, and thereafter an increasing value which has no basis in the observed data — so extrapolation of the model to Sierra Nevada population would be inappropriate.

In cases where a species distribution is discontinuous, or materially influenced by edaphic or biotic factors, it is simplistic to expect that any indices of geographic location will adequately represent variation in the selection pressures responsible for differentiating the population. Climatic records may provide useful indices, though good data is frequently lacking for forest regions, or it may be necessary to make more detailed investigations of the operational environmental factors (Waring and Major 1964) at each seed collection site. The cost of such an exercise may appear prohibitive, but the reward, through application of the resulting growth models, will be a reduced necessity for continual planting of empirical provenance trials.

Acknowledgements

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Literature Cited

Birot, Y.: Variabilité infraspecifique du poids de la graine chez le Douglas. Silvae Genetica 21 (6), 240—253 (1972). — Buck, J. M. *et al.*: California tree seed zones, U.S.D.A. For. Serv. California Region, San Francisco. 5 p. (1970). — Griffin, A. R.: Geographic variation in juvenile growth characteristics of Douglas-fir from the coastal ranges of California. Ph. D. Thesis. Corvallis, Oregon, O.S.U. 153 pp. (unpubl.) (1974). — Griffin, A. R., and K. K. Ching: Geographic variation in Douglas-fir from the coastal ranges of California. I. Seed, seedling growth and hardiness characteristics. Silvae Genetica 26 (5/6) (1977). — Hattemer, H. H. and A. König: Geographic variation of early growth and frost resistance in Douglas-fir. Silvae Genetica 24 (4), 97—106 (1975). — Rout, A. F.: Establishment report ACT/S/TB/2 no. 26 For. Res. Inst. Canberra (1973) (unpubl.). — Rowe, K. E., and K. K. Ching: Provenance study of Douglas-fir in the Pacific Northwest II. Field performance at age nine. Silvae Genetica 22 (4), 115—119 (1973). — Silen, R. R.: The 1912 Douglas-fir heredity study. U.S. Forest Service PNW For. & Range Expt. Sta. Ann. Rep. 1963 (1964). — Sweet, G. B.: Provenance differences in Pacific Coast Douglas-fir. Silvae Genetica 14 (1), 46—56 (1965). — Sziklai, O.: Variation and inheritance of some physiological and morphological traits in Douglas-fir U.S.F.S. Res. Paper N.C. For. Expt. Sta. No. NC-6 (1966). — Waring, R. H., and J. Major: Some vegetation of the Californian coastal redwood region in relation to gradients of moisture, nutrients, light and temperature Ecological Monographs 34, 167—215 (1964). — Wilcox, M. D.: Douglas-fir provenance variation and selection in New Zealand. N.Z. For. Serv. F.R.I. Genetics and Tree Imp. Report 69 (unpubl.) (1974).

Altitudinal variation in germination characteristics of yellow-poplar in the southern appalachians[1]

By P. E. Barnett and R. E. Farmer, Jr.[2])

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Summary

Open-pollinated seed from parent trees located at high and low elevations in the southern Appalachians were germinated in factorial trials to develop germination procedures for genetically variable yellow-poplar. Test factors included light, temperature, stratification procedure, and collection time, all of which significantly influenced germination percentage. The main source of variation, however, was the elevation of parent trees, with high elevation families exhibiting substantially lower germination than did low elevation families. Significant variation was also noted among families within elevational provenances. Stimulation of germination of the majority of seed from high elevation parents could be attained only through long stratification periods (18 months). Gibberellins were sporadically effective in stimulating germination of unstratified seed from some families.

Key words: Stratification, light, temperature, collection date, and gibberellin.

Zusammenfassung

Saatgut von *Liriodendron tulipifera* L. aus einigen Provenienzen unterschiedlicher Seehöhe in den südlichen Appalachians wurde zu Keimversuchen mit verschiedenen Testfaktoren herangezogen. (Licht, Temperatur, Stratifikation und Zeitpunkt der Saatguternte). Als Hauptursache für die Variation der Herkünfte stellte sich die Höhe ü. NN der Ausgangsbäume heraus. Dabei zeigte das Saatgut aus höheren Lagen, über 1000 m, ein niedrigeres Keimprozent als solches aus tieferen Lagen, 270—470 m. Eine Stimulation der Keimung konnte nur durch Stratifikation erreicht werden. Die Anwendung von Gibberellin hatte bei nicht stratifiziertem Saatgut teilweise sporadischen Einfluß.

Introduction

Although seed handling recommendations for yellow-poplar *(Liriodendron tulipifera* L.) have been published for decades (TVA 1940; Bonner and Russell 1974) and dormancy relations are known in a general way (Adams 1968; Boyce and Hosner 1963; Clark and Boyce 1964), recent nursery experience in connection with breeding programs has highlighted problems of predicting germination for individual open-pollinated and full-sibling progenies. For example, some stratified or fall-planted seed lots have failed to germinate adequately in the year of planting, but have produced seedlings abundantly the second year. Difficulty with progeny test establishment has been a result.

Yellow-poplar seed may remain in the litter (Clark and Boyce 1964) or stratified in soil pits (Williams and Mony 1962) for several years, with increasing germination capacity developing over time. Such a reproductive strategy has considerable fitness value for an intolerant species. Working with seed from a single tree in southern Illinois, Boyce and Hosner (1963) noted that several cycles of chilling followed by warm temperature resulted in complete germination over a six-month period. This suggested intra-family variation in chilling requirement, with a portion of the family requiring a single cycle and another portion two or more cycles. On the other hand, the work of Adams (1968) with a Virginia source indicated that complete germination could be obtained with a single 20-week exposure to a chilling temperature and that weekly alternatives from 36° to 54° F (2°—12° C) resulted in reduced germination relative to constant chilling. Hence, it is still unclear whether yellow-poplar seed requires a single long period of chilling or several cycles of chilling followed by germination temperatures, or whether these two strategies are interchangeable. Patterns of natural variation in dormancy are not known, though such variation appears to be a dominant factor in germination. This investigation is aimed at clarification of these questions using open-pollinated seed from individual trees of altitudinally diverse provenances in the southern Appalachian mountains.

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